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Experimental selection for calving ease and postnatal growth in seven cattle populations. I. Changes in estimated breeding values

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Experimental selection for calving ease and postnatal growth in seven cattle populations. I. Changes in estimated breeding values[1,2]

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ABSTRACT: Selection was used to create select and control lines within 4 purebred and 3 composite cattle populations. Both lines were selected for similar direct yearling weight and maternal weaning weight EBV. Select lines were selected for lower 2-yr-old heifer calving difficulty score EBV and control lines were selected for average birth weight EBV. Select (n = 6,926) and control (n = 2,043) line calves were born from 1993 through 1999 and selection began with the 1992 mating. High replacement rates resulted in 2,188 births to select line and 598 births to control line heifers. Data used to calculate EBV came from these populations and from 15 yr of data preceding the experiment. Calving difficulty was scored from 1 (no assistance) to 7 (cesarean). Calving difficulty scores from all twins, malpresentations, and cows 3 yr old and older were eliminated. Except for the first year, when a single-trait BLUP was used, a multiple-trait BLUP was used to calculate direct and maternal EBV for calving difficulty score, birth weight, and weaning weight, and direct EBV for postweaning gain. Sires (n = 498) were selected from those born in both the preceding populations and the select and control lines. In purebred populations, some industry sires (n = 88) were introduced based on their EPD. Tests of mean select and control line EBV differences of calves born in the final 2 yr were based on population variation. Select line direct EBV were 1.06 lower for heifer calving difficulty score ($P < 0.001$) and 3.5 kg lower ($P < 0.001$) for birth weight than controls. Average differences for other EBV were small and not significant. Yearling weight EBV was intentionally increased in both select and control lines of purebred populations. Angus, Hereford, Charolais, and Gelbvieh yearling weight EBV in control lines increased by 32.4, 27.2, 21.0, and 10.5 kg, respectively, from 1991 and 1992 to 1998 and 1999 compared with an average increase of 2.7 kg in composite populations. Birth weight direct EBV in purebred control lines increased by approximately 8% of yearling weight EBV increases. Selection based on a multiple-trait BLUP was able to create lines differing in calving difficulty score and birth weight EBV, but not in weaning weight and postweaning gain EBV. Differences between lines should be useful for evaluating BLUP and other traits and for identifying potential limitations of genetically decreasing calving difficulty score and birth weight.

Key words: birth weight, calving difficulty, cattle, estimated breeding value, genetic trend, selection

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INTRODUCTION

Calving difficulty in first-calf heifers is typically greater than in older multiparous cows. For instance, Gregory et al. (1991a) reported that first-calf heifers had nearly 50% more calving difficulty than mature cows. Brinks et al. (1973) and Laster et al. (1973) found that dystocia decreased the survival of calves and caused a reduction in probability of subsequent conception. Rogers et al. (2004) found that cows experiencing dystocia were at a 58% greater risk of subsequent culling.

Response to simple selection for heifer calving ease would be slow, because the trait is observed only in calves born to heifers and heritability is low to moderate (Koots et al., 1994; Bennett and Gregory, 2001a). However, heifer calving ease is highly correlated with birth weight and moderately correlated with other weights measured on most animals in a herd (Bennett and Gregory, 2001a). Selection using multiple-trait BLUP accounting for both correlated traits and measurements on relatives should increase the selection

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[2]Mention of trade name, proprietary product, or specified equipment does not constitute a guarantee or warranty by the USDA and does not imply approval to the exclusion of other products that may be suitable.

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response well beyond simple selection for heifer calving ease.

Selection only for calving ease would decrease growth, especially when calving ease breeding value predictions incorporate correlated weight traits. Selection indexes and schemes that mitigate correlated changes in growth have been proposed (Dickerson et al., 1974; Foulley, 1976) and experimentally evaluated (Arnold et al., 1990; MacNeil et al., 1998; MacNeil, 2003).

The objective of this research was to estimate changes in breeding value in beef cattle experimentally selected for improved calving ease while maintaining or increasing growth by using EBV predicted from multiple-trait BLUP. Results will determine the genetic response realized through multiple-trait selection on moderately to highly antagonistic traits.

MATERIALS AND METHODS

The US Meat Animal Research Center Animal Care and Use Committee approved the procedures used in this experiment.

Populations

The Germ Plasm Utilization (**GPU**) experiment at the US Meat Animal Research Center, Clay Center, NE (Gregory et al., 1991a), compared 9 purebred and 3 composite populations from 1978 through 1992 and was then terminated. Four purebred (Angus, Charolais, Gelbvieh, and Hereford) and 3 composite (MARC I, MARC II, and MARC III) populations were transferred to this experiment. Some animals from other US Meat Animal Research Center sources were also added to increase population sizes.

Two lines (select and control) were formed in each of the 7 populations. The 2 lines were intended to contrast breeding value selection for decreased 2-yr-old calving difficulty with no change in calving difficulty. Details of selection differed by population and are described in a subsequent section. Herd size was approximately 150 calving females (including 45 two-year-old heifers) for each select line and 42 calving females (including 12 two-year-old heifers) for each control line. The first selected parents were mated in 1992 and 6,926 select and 2,043 control calves were born from 1993 through 1999.

Purebred and composite populations both used bulls and semen from bulls born within these lines. In addition, the purebred and composite populations both used GPU bulls that were alive in 1992 and semen collected through 1992. When the experiment started, 29 Angus, 24 Charolais, 27 Gelbvieh, 19 Hereford, 84 MARC I, 66 MARC II, and 37 MARC III sires used in GPU had more that 15 units of semen remaining in frozen storage. Because bulls born in GPU before 1993 were not assigned to lines, these bulls were used based on their EBV. The EBV of 30 GPU bulls used in a line changed enough during the experiment that they were subsequently used in the other line. When this happened, progeny remained in the line designated at the time of mating.

The purebred populations used some sires introduced from the industry. Purebred bulls introduced from the industry were assigned to control or select lines. In Herefords, a group of bulls obtained from a single source before the experiment began, and not clearly compatible with either control or select criteria, were used in both lines to a limited extent based on within-herd EBV.

Approximately 15 select and 6 control AI and natural service sires were bred to females each year, minimizing matings of close relatives. Select line AI sires were used until semen supplies were depleted or sires with better EBV became available. Select line natural service sires were retained until younger sires with better EBV were available or they became unsound. Control line AI and natural service sires were replaced more quickly and used on fewer females than select line sires in an effort to increase effective numbers. Total numbers of unique bulls used were 351 (53 industry) in select lines and 235 (35 industry) in control lines.

Before selection in 1992, 109 Angus, 155 Charolais, 102 Gelbvieh, 116 Hereford, 233 MARC I, 221 MARC II, and 240 MARC III cows were assigned to the experiment. Before selection in 1992 and in 1993, 276 Angus, 114 Charolais, 78 Gelbvieh, 174 Hereford, 202 MARC I, 200 MARC II, and 185 MARC III yearling heifers born in 1991 or 1992 were assigned to the experiment. In populations with an excess of females assigned, females were first assigned to control lines based on control line criteria and sire. The remaining cows were assigned to select lines, and the desired number was retained based on select line criteria and sire. In the Gelbvieh population, females were assigned to control and select lines at random within sire. Some cows (388) produced progeny born in both lines during the first 3 yr. Cows were changed to a different line based on updated EBV and a desire to maintain high effective numbers of parents in the smaller control lines. When cows' lines were changed, their calves remained in the lines designated at breeding. Cows remained within the lines designated for the 1994 breeding season for subsequent years. Cows in select and control lines were culled based on a negative pregnancy diagnosis, on EBV selection criteria, and on health and temperament.

Management

Yearling heifers were bred AI for approximately 21 d, followed by natural service bulls in individual pastures for approximately 42 d. Only yearling bulls were bred by natural service to yearling heifers. Approximately 3 wk after beginning AI mating of heifers, cows 2 yr old and older were bred AI for 21 d, followed by natural service bulls 2 yr old and older in individual pastures for approximately 42 d. Sires used for AI mating were used for both heifers and older cows. In 1996 and 1997, 12 to 13% of cows (1 select line sire mated to 24 cows and 1 control line sire mated to 7 cows in each population) were bred only by natural service bulls in single-sire pastures for the entire 9-wk breeding season.

Except when cows and their calves were in single-sire pastures, select and control line females from the same population were mixed within contemporary calving groups. Average calving dates were March 15 for 2-yr-old heifers and April 6 for cows 3 yr old and older. Heifers calving as 2 yr olds averaged 712 d of age (90% of heifers calved between 674 and 753 d of age). A mixture of corn silage and alfalfa haylage, along with alfalfa and grass hay, was fed to 2-yr-old females starting approximately 2 mo before calving and continuing until adequate pastures were available, usually in middle to late April. Older females were fed limited quantities of corn silage and alfalfa haylage to meet nutrient requirements from November until mid- to late April.

The average weaning date was October 14. Average weaning ages of calves were 212 d (yearly averages from 200 to 225 d) from 2-yr-old heifers and 190 d (yearly averages from 177 to 203 d) from cows 3 yr old and older. After an initial adjustment feeding period of approximately 42 d, females were fed diets composed of corn silage, alfalfa haylage, and a protein-mineral-vitamin supplement in various proportions (approximately 2.2 to 2.3 Mcal of ME/kg of DM) and lengths of time, depending on weather conditions and weight gains, until they were placed on improved cool-season grass pasture from mid- to late April. Hereford heifer calves born in 1998 and 1999 were managed differently and were fed for slaughter after weaning. After a 42-d adjustment period after weaning, males were fed a diet composed of corn silage, rolled corn, and a protein-mineral-vitamin supplement (approximately 2.7 Mcal of ME/kg of DM).

Calves were weighed at birth, at weaning, and at 148 d after weaning (yearly averages from 140 to 157 d). Yearling heifers were weighed when they were palpated for pregnancy. Subsequently, females were weighed, measured for height, and scored for condition before calving, at the start of breeding season, and when they were palpated for pregnancy (3 to 21 d after weaning) each year.

Calving difficulty was subjectively evaluated by field personnel trained each year for accuracy and consistency of calving difficulty scores. The following descriptive scores were used: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with a calf jack, 4 = slight difficulty with a calf jack, 5 = moderate difficulty with a calf jack, 6 = major difficulty with a calf jack, 7 = cesarean birth, and 8 = abnormal presentation.

Selection

Data. Four traits were used in the EBV analysis: calving difficulty score for 2-yr-old heifers, birth weight, weaning weight adjusted to 200 d, and postweaning gain adjusted to 168 d. Actual weaning weights were adjusted to 200 d, assuming linear growth from birth to weaning. Postweaning gain was adjusted to 168 d, assuming linear growth from weaning to yearling weight measurement. Heifer calving difficulty scores were set to missing values for all calves born to cows 3 yr old and older and for any calf scored an 8. All twin calf data and weaning weights and postweaning gains of fostered calves were set to missing values for analysis.

EBV. Single-trait analyses for EBV were used to make selections in 1992 and 1993. Subsequently, EBV were estimated from a 4-trait animal model by using MTDFREML (Boldman et al., 1995). Direct genetic effects were modeled for all 4 traits. Maternal genetic effects were modeled for heifer calving difficulty score, birth weight, and weaning weight. Permanent environmental effects attributable to dams were modeled for birth and weaning weights. Estimated (co)variances (Bennett and Gregory, 2001a) were used for random effects. Fixed contemporary groups were defined by combinations of year of birth, sex, and management group. Age of dam (2, 3, 4, and 5 yr or more) was fitted with linear and quadratic regression coefficients. In purebred populations, genetic groups (USMARC source, select industry source, and control industry source) were used (Westell et al., 1988). In Herefords, there was an additional grouping for the bulls obtained from a single source before the beginning of the experiment.

Each population was analyzed independently, including data from GPU and other contributing experimental sources beginning in 1978. Each population was analyzed ignoring line (select or control).

Selection Procedures. The selection goals were the creation of 2 lines for each population with similar growth to yearling age, but with improved heifer calving ease in one line. The lines were created by using an ad hoc multistage selection procedure based on multitrait EBV. The objectives of the ad hoc procedure were similar to those of the restricted and desired gain indexes (Brascamp, 1984), but it was unclear how these indexes could be applied directly in this complex situation with different sire sources, multiple generations, and multistage selection using EBV.

Every year, EBV were analyzed 3 times. Each time, target EBV for maternal genetic weaning weight and direct genetic yearling weight were identified for each population. The same EBV targets were used in both selection and control lines within populations. In select lines, animals were selected with the lowest EBV for calving difficulty score and with EBV for maternal genetic weaning weight and direct genetic yearling weight within an acceptable range around their target EBV. In control lines, target EBV for direct genetic birth weight were identified in each population that would result in birth weight changes proportionally similar to yearling weight changes. The proportion was determined from phenotypic averages for birth and yearling weights. Animals in control lines were selected from those with EBV within an acceptable range around targets for direct genetic birth weight, maternal genetic weaning weight, and direct genetic yearling weight. Additional constraints on numbers of half-sibs selected were used to maintain a broad pedigree. Usually no more than 2 sons per sire were retained in select lines and 1 son per sire was retained in control lines. In addition, in the early stages of introducing industry sires, genetic group values were poorly estimated, especially for maternal effects. Some progeny of introduced sires were initially retained and used, ignoring poorly estimated EBV.

Target EBV for maternal genetic weaning weight and direct genetic yearling weight were determined differently for purebred and composite populations. Target EBV for composites were set to be similar to mean EBV at the end of the GPU experiment. Many industry purebred populations had substantially increased yearling weight and milk EPD from 1978 to 1992. Purebreds in the GPU experiment were not selected for growth during this period (Gregory et al., 1991a). Therefore, target EBV for purebred populations were set to increase genetic levels of growth and maternal weaning weights in the purebred populations toward those in industry. Growth and maternal weaning weight targets in purebreds were increased each year. The intention was to increase EBV for these traits by at least two-thirds of the change that occurred in industry herds from 1978 to 1992. Target EBV for birth weight was set to be in the same proportion to yearling weight EBV targets as the phenotypic proportion. Proportionality of control line birth weight and yearling weight EBV targets was applied only to the EBV means of selected animals and not to individual animal EBV. Maintaining the ratio of birth weight to yearling weight was done in an attempt to minimize changes in the genetic level of heifer calving difficulty in the control lines.

Heifer calving difficulty score maternal and direct EBV were weighted differently for selection in different populations. A "terminal" weighting of 0:1 maternal to direct was used in Charolais and MARC I. A "general purpose" weighting of 1:1 maternal to direct was used in Gelbvieh and MARC II. A "maternal" weighting of 2:1 maternal to direct was used in Angus, Hereford, and MARC III. Weightings were applied to unstandardized direct and maternal calving difficulty score EBV.

Purebred industry bulls used in select and control lines were further selected for above-average EPD for yearling weight and milk to make the experimental populations closer to industry growth and milk EPD. Industry Angus, Charolais, and Hereford bulls used in select lines had low birth weight EPD. Gelbvieh bulls were chosen for desirable calving ease EPD. Industry purebred bulls used in control lines were selected for birth weight EPD that was proportionally similar to yearling weight EPD.

Figure 1 illustrates the main features of selection among MARC II males born in 1997 after weaning and after yearling EBV calculations. A common target EBV for yearling weight was used for select and control lines. Control and select line bulls selected as yearlings had similar average yearling weight EBV. Control line EBV for birth weights of selected yearling bulls were near their target EBV.

An analysis to calculate EBV was conducted in late autumn after weaning. These EBV were used to identify 16 select line and 6 control line weaned males to be left intact for potential selection at yearling age. Additional weaned males were selected and left intact for other uses. The remaining males were castrated. These EBV were also used to cull cows and to retain 6 select and 2 control line bulls aged 18 mo and older for the following year. A second analysis to calculate EBV was conducted after yearlings were weighed. These EBV were used to select 6 select line and 3 control line yearling bulls and 50 select line and 15 control line heifers. A third analysis to calculate EBV was conducted after 6 to 8 wk of calving, including newly collected birth weight and heifer calving difficulty scores. These EBV were used to make decisions on the use of live and AI bulls for breeding. As many as 100 units of semen were collected from bulls used for breeding.

Selection of heifers born in 1996 and 1997 was relaxed. Heifers retained for breeding were randomly selected within sire. Relaxation of selection allowed the evaluation of 2-yr-old heifer calving difficulty in 1998 and 1999 unbiased by possible phenotypic effects of selection for EBV.

Statistical Analyses of EBV

Differences between select and control line EBV were evaluated for animals born in 1998 and 1999. The following model was fitted by using the MIXED procedure (SAS Inst. Inc., Cary, NC):

$$Y_{klm} = LINE_k + POP_l + LINE_k \times POP_l + \varepsilon_{klm},$$

where Y_{klm} is the direct EBV for calving difficulty score, birth weight, weaning weight, or postweaning gain, or maternal EBV for calving difficulty score, birth weight, or weaning weight; $LINE_k$ is the select or control; POP_l is the population; and ε_{klm} is the residual error for the mth animal in the kth line and lth population. Population and the interaction of line × population were considered random. Line differences (select line minus control line) were tested for significance with the *F*-test. The Satterthwaite method was used to determine degrees of freedom.

RESULTS

A total of 8,969 calves with valid data were born (Table 1). An intentionally high cow replacement rate was desirable and resulted in 31% of calves born to 2-yr-old dams. More heifers were scored for calving difficulty, making more selection among females and a decreased generation interval possible. This was expected to result in more accurate heifer calving difficulty EBV, in-

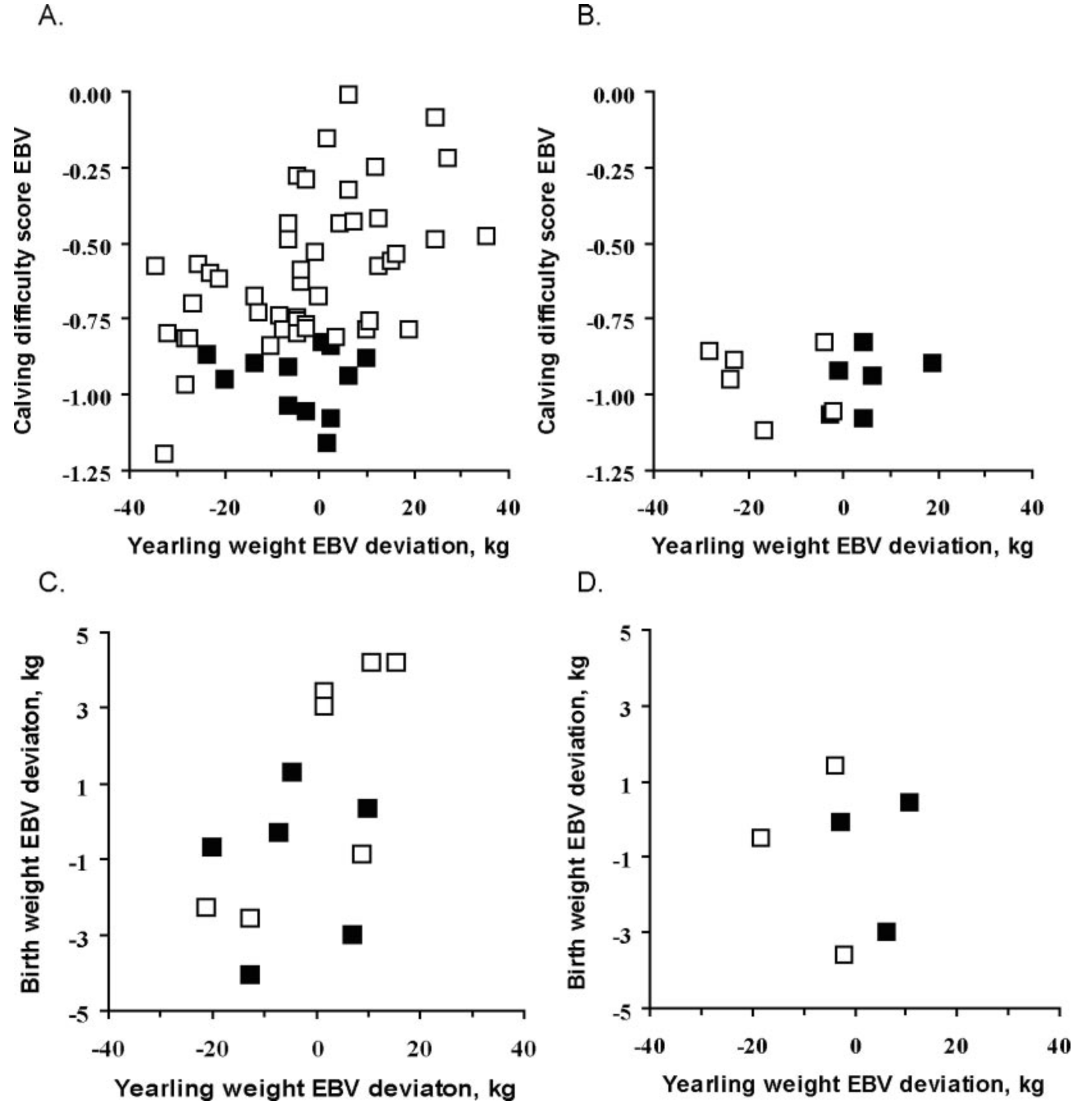

Figure 1. Ad hoc selection of MARC II select (A, B) and control (C, D) males born in 1997 after weaning (A, C) and after yearling weights (B, D) is shown. The abscissas show yearling weight EBV deviations from the MARC II goal. The ordinates show heifer calving difficulty score EBV for the select line or birth weight EBV deviation from the MARC II control line goal. Filled squares (■) represent males selected to remain intact after weaning and after yearling EBV calculations. Open squares (□) represent intact males not selected.

creased genetic change, and more accurate measurement of phenotypic trends.

Detailed use of 586 sires is shown in Table 2. Select line sires were used an average of 2.1 yr and had 19.7 progeny. Control line sires were used for 1.2 yr and averaged 8.7 progeny. Fewer progeny per sire in the control line partially compensated for expected larger genetic drift from having fewer cows in the control lines. In purebred populations, 27% of select line sires and 25% of control line sires were introduced from industry. Introduced sires were 15% of all sires used in Gelbvieh, 18% in Charolais, 34% in Angus, and 38% in Hereford. Differences in use partially reflected differences among industry purebred population EPD trends from 1977 through 1992 and therefore expected differences between experimental and industry populations. More industry sires were used in Angus and Herefords, because the differences between industry and the experimental populations were thought to be the largest in those breeds.

Ignoring subsequent selection of original cows calving in 1993, select line calves born in 1998 and 1999 averaged 1.56 generations of selection. If heifers born in 1996 and 1997 had been selected instead of randomly retained, generations of selection would have approached 2.0. The maternal grandsires of 88% of select line calves born in 1998 and 1999 were selected sires.

Select and Control Differences

Average EBV trends show (Figure 2) that most selection objectives were achieved. Average EBV for the final 2 yr (1998 and 1999) are shown in Table 3. The average difference between lines (select minus control)

Table 1. Number of calves born by population, line, age of dam, and birth year

Population	Line	Age of dam	Birth year 1993	1994	1995	1996	1997	1998	1999	Total
Angus	Select	2-yr	129	48	42	46	34	45	39	383
		All	198	151	154	154	150	153	144	1,104
	Control	2-yr	19	11	14	13	14	15	11	97
		All	43	47	47	44	45	44	40	310
Charolais	Select	2-yr	32	37	42	44	40	42	39	276
		All	126	144	131	119	126	139	143	928
	Control	2-yr	6	10	15	8	9	14	12	74
		All	34	24	41	40	37	44	45	265
Gelbvieh	Select	2-yr	25	27	27	37	42	44	50	252
		All	76	100	110	129	129	121	144	809
	Control	2-yr	3	4	12	14	12	9	9	63
		All	39	33	37	38	36	40	35	258
Hereford	Select	2-yr	44	31	49	43	38	48	37	290
		All	132	139	147	155	140	136	122	971
	Control	2-yr	30	12	9	17	9	12	10	99
		All	37	48	46	42	41	40	35	289
MARC I	Select	2-yr	49	47	46	44	41	44	45	316
		All	172	138	124	130	127	140	143	974
	Control	2-yr	21	10	12	13	13	13	10	92
		All	65	39	42	41	40	41	37	305
MARC II	Select	2-yr	68	47	49	44	40	46	49	343
		All	179	143	131	130	129	160	159	1,031
	Control	2-yr	20	10	13	13	14	8	11	89
		All	70	38	42	37	41	45	43	316
MARC III	Select	2-yr	65	48	42	44	42	43	44	328
		All	185	170	157	157	153	147	140	1,109
	Control	2-yr	10	10	13	13	12	13	13	84
		All	41	37	45	53	41	41	42	300
Total	Select	2-yr	412	285	297	302	277	312	303	2,188
		All	1,068	985	954	974	954	996	995	6,926
	Control	2-yr	109	67	88	91	83	84	76	598
		All	329	266	300	295	281	295	277	2,043

in calving difficulty score direct EBV was −1.06. The direct EBV difference for the highly correlated trait, birth weight, was −3.5 kg. Line differences for weaning weight direct and maternal EBV and yearling weight direct EBV were small and not significant.

Table 2. Sire use and numbers of unique and introduced industry sires

Breed	Line	Sires/yr	Unique[1]	Industry[2]
Angus	Select	16.7	53	18
	Control	6.0	42	14
Charolais	Select	14.9	53	10
	Control	5.6	32	5
Gelbvieh	Select	13.0	43	7
	Control	5.4	38	5
Hereford	Select	14.1	47	18
	Control	6.1	30	11
MARC I	Select	15.3	51	—
	Control	6.1	39	—
MARC II	Select	15.3	51	—
	Control	6.4	39	—
MARC III	Select	15.1	53	—
	Control	5.7	35	—
Total	Select	105.0	351	53
	Control	41.4	235	35

[1]Many sires were used more than 1 yr.

[2]Sires introduced from industry. None were introduced into composite populations.

The line difference in maternal EBV for calving difficulty score was small and not significant, even though it was included in the weighted calving difficulty score EBV for 5 of the 7 populations. Reasons for this were that maternal heritability was half that of direct heritability and the genetic correlation of maternal and direct effects was −0.3, that no traits highly correlated with maternal heifer calving difficulty score were identified or included in the multitrait EBV analysis (Bennett and Gregory, 2001a,b), and that there are fewer maternal expressions of heifer calving difficulty score than expressions of birth weight, which is highly correlated with direct heifer calving difficulty. For these reasons, variation in maternal EBV was much less than direct EBV. Therefore, even a 2:1 maternal-to-direct EBV weighting did not result in much change in maternal EBV.

Another important reason for no average difference in maternal EBV for calving difficulty score was the introduction of industry sires into the purebred populations. Sires introduced for the 1992 breeding season did not have any daughters calving until 1995. The industry genetic groups typically had too few 2-yr-old daughters

Table 3. Line differences (select line minus control line) in EBV for calves born in 1998 and 1999, averaged over 7 populations

EBV trait	Type[1]	Difference	F-value	P[2]
Heifer calving difficulty score	D	−1.06	78.9	<0.001
	M	−0.05	0.13	0.73
	D + M	−1.11	93.8	<0.001
Birth weight, kg	D	−3.5	77.0	<0.001
	M	−0.1	0.95	0.37
	D + M	−3.7	67.4	<0.001
Weaning weight, kg	D	0.5	0.21	0.66
	M	0.1	0.08	0.84
	D + M	0.6	0.39	0.55
Postweaning gain, kg	D	0.0	0.00	0.98
Yearling weight,[3] kg	D	0.5	0.08	0.79
	D + M	0.6	0.17	0.69

[1]D = direct EBV; M = maternal EBV; D + M = sum of direct and maternal EBV.
[2]Satterthwaite df for the F-value ranged from 5.99 to 6.12.
[3]Yearling weight EBV is the sum of weaning weight and postweaning gain EBV.

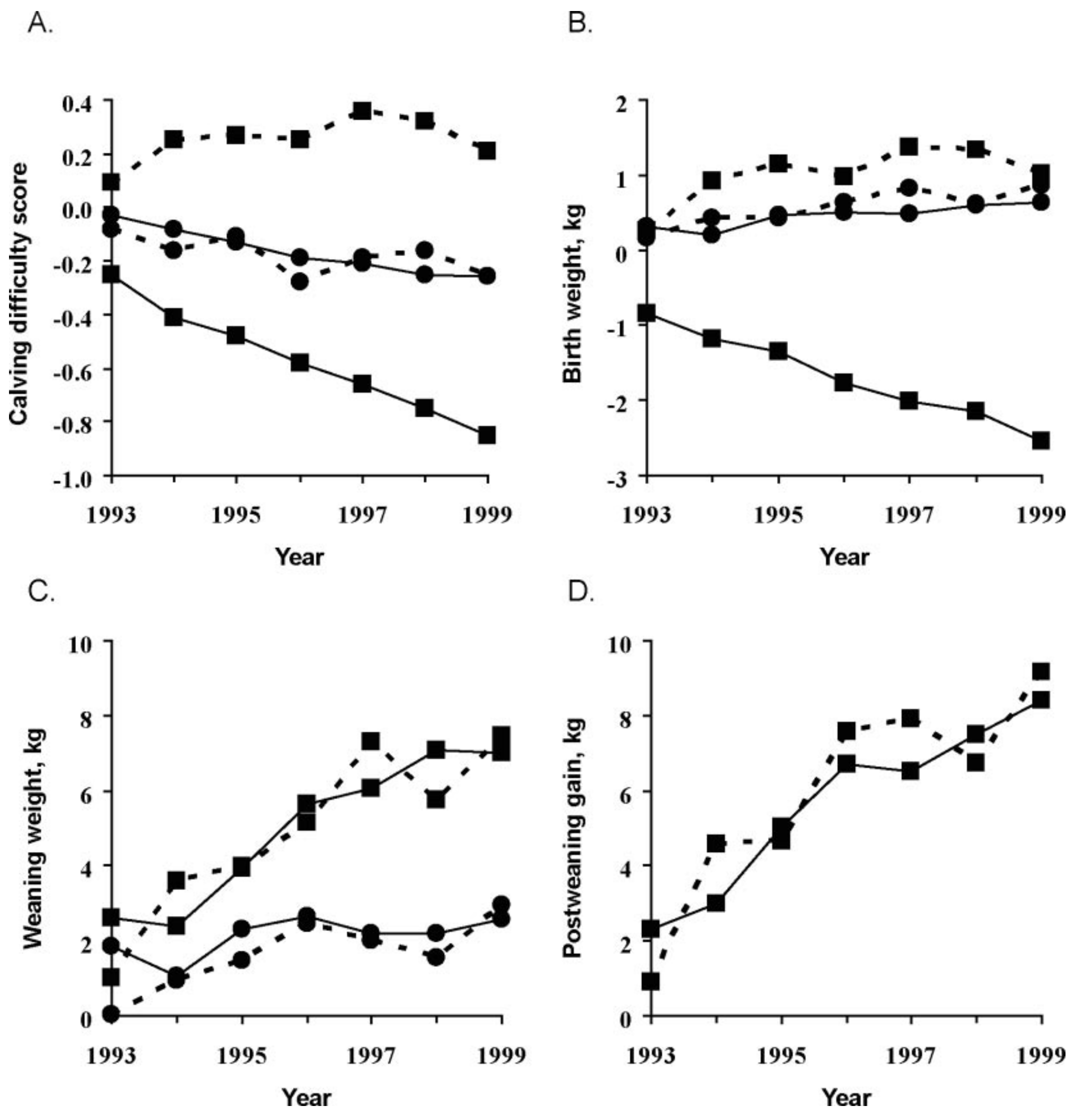

Figure 2. Trends in select (solid lines) and control (dashed lines) lines for direct (■) and maternal (●) EBV averaged over 7 populations are shown. Traits are (A) heifer calving difficulty score, (B) birth weight, (C) weaning weight, and (D) postweaning gain. All EBV are differences from the 1991 and 1992 averages.

Table 4. Differences (select line minus control line) in heifer calving difficulty score EBV for composite and purebred populations and maternal:direct EBV weights

EBV	Population type	Maternal:direct EBV weights[1]		
		0:1	1:1	2:1
Maternal	Purebred	−0.05	−0.23	0.34
	Composite	0.12	−0.43	−0.42
Direct	Purebred	−1.08	−0.80	−1.19
	Composite	−1.30	−1.30	−0.60

[1]Average of select minus control line differences by population type and maternal:direct EBV emphasis. Purebred populations and their ratios of maternal:direct weighting of heifer calving difficulty EBV are Charolais (0:1), Gelbvieh (1:1), and Angus and Hereford, (2:1). Composite populations are MARC I (0:1), MARC II (1:1), and MARC III (2:1).

calving to accurately estimate their group effects until the middle or later years of the experiment. Averages by population and line for maternal and direct EBV for 1998 and 1999 (Table 4) showed that composites with nonzero maternal EBV weightings had maternal EBV differences in the expected direction, but purebred maternal populations were not consistent. Introducing industry sires resulted in inaccuracies in maternal EBV in the first half of this relatively short selection experiment and affected selections based on these EBV.

There were no differences between select and control lines for weaning and postweaning gain EBV. However, both select and control line EBV for these traits changed from the 1991 and 1992 averages as intended. Control line averages (Table 5) showed large changes in maternal weaning weight and direct yearling weight EBV for purebred populations, especially Angus and Hereford, but small changes in composites. Industry Angus and Hereford showed large changes in growth and milk EPD from 1977 to 1992. Changes in 2 × EPD for milk and yearling weight during that period were 7 and 40 kg for Angus (http://www.angus.org/sireeval/genetic.html, accessed 3/7/2006) and 5 and 32 kg for Hereford (http://www.hereford.org/Acrobat/Perf/S06_Trend.pdf, accessed 3/7/2006), respectively. Changes in the experimental populations (Table 5) were 80% or more of the 1977 to 1992 changes in industry Angus and Hereford for these traits.

Table 5. Differences between averages of 1998 and 1999 EBV and 1991 and 1992 EBV for direct birth weight EBV in control lines and for maternal weaning and direct yearling weight EBV combined across lines

Population	Average 1998 and 1999 control line EBV[1]		
	Direct birth weight,[2] kg	Maternal weaning weight,[3] kg	Direct yearling weight,[3] kg
Angus	1.2	7.4	32.4
Charolais	2.8	6.6	21.0
Gelbvieh	0.9	0.1	10.5
Hereford	1.9	4.0	27.2
MARC I	0.4	−0.1	6.4
MARC II	0.1	0.3	−3.5
MARC III	0.0	0.5	5.1

[1]Difference from average of 1991 and 1992 EBV.
[2]Differences only in control lines.
[3]Differences were combined across control and select lines.

In purebred control lines, changes in direct birth weight EBV were intended to be proportional to changes in yearling weight EBV. Increases in direct birth weight EBV of purebred control lines averaged 7.9% of direct yearling weight EBV changes. This was less than the phenotypic birth weight-to-yearling weight proportion of 10.4% in 1991 and 1992. The sum of direct and maternal birth weight EBV changes divided by the sum of changes in maternal weaning weight EBV and yearling weight EBV resulted in a ratio of 10.3%.

DISCUSSION

Successful antagonistic selection (selection of traits in directions that are opposite the genetic correlation) has been demonstrated in the mouse (e.g., Cockrem, 1959; Rutledge et al., 1973; Atchley et al., 1997). These antagonistic selection experiments generally used phenotypic index selection, a single stage of selection, and had discrete generations.

In cattle, most reported experiments have used single-trait selection or index selection with a mildly antagonistic objective. Exceptions to this include 2 selection experiments for birth and yearling weights (MacNeil et al., 1998; MacNeil, 2003). In the first experiment, a 2-stage independent culling process was used to first select for below-average birth weight and then for high yearling weight. This resulted in small changes in birth weight and lower birth and yearling weights than did single-trait selection for yearling weight. The second experiment based selection on the index of Dickerson et al. (1974; yearling weight − 3.2 × birth weight) compared with an unselected control line. This selection resulted in small positive increases in birth weight and moderate positive increases in yearling weight. Arnold et al. (1990) reported the results of selecting 5 low-birth-weight sires and 4 high-birth-weight sires, all with similar high yearling weights, based on industry EPD. Progeny had differences in birth weight and yearling weight similar to their EPD. The results reported in Table 4 and Figure 2 clearly show antagonistic average responses of decreased birth weight and increased yearling weight.

This experiment is a practical application of strongly antagonistic selection in beef cattle when using currently available breeding value estimation technology and resources. It incorporates the multiple sources, generations, and stages of selection using breeding values estimated from multiple, correlated traits. This experimental strategy is not appropriate for estimating realized heritabilities or genetic correlations in the way that model organisms and some livestock have been used. Instead, the lines are best used to verify the usefulness of EBV, to estimate correlated responses in traits with low heritabilities, and to evaluate potentially undesirable, nonlinear responses correlated to large genetic changes in primary traits.

Sorensen et al. (2003) recommends using control lines when estimating response to selection, even if likelihood analyses are to be used. Both select and control lines were included in this experiment, but control lines were not random. Instead, control lines were selected toward specific EBV goals to make desired contrasts with select lines. Control lines had many fewer cows than did select lines. However, AI and semen from GPU and industry still allowed many sires to be used. Variability of EBV means was larger in the control line (Figure 2), but trends were still clear.

Estimated breeding value differences resulting from selection clearly showed that cattle can be simultaneously selected for increased growth and less calving difficulty. The resulting select and control lines differed by approximately 0.8 genetic SD for calving difficulty score and 0.9 genetic standard deviations for birth weight. On average, yearling weight increased by more than 0.5 genetic standard deviation, but exceeded 1 genetic standard deviation in Angus and Herefords. Differences between lines should be large enough to evaluate correlated changes in the 4 main traits and other traits and to identify potential limitations of genetically decreasing calving difficulty score and birth weight. Unlike many examples of genetic differences in calving difficulty and birth weight, differences between these lines should not be partially or completely confounded with subsequent growth rates.

The primary approaches for improving genetic potential for beef cattle production are selection among populations, mating systems that utilize complementarity and heterosis, and selection within populations. All these tools should be used to enhance production. Different production traits are more easily addressed with different approaches. The antagonistic relationship between postnatal growth and birth weight among breeds limits selection among breeds as an effective tool for increasing growth and reducing calving difficulty, except for the use of *Bos indicus* dams, which can reduce the birth weight of *Bos taurus*-sired calves (e.g., Amen et al., 2007). Heterosis increases growth, birth weight, and calving difficulty (Gregory et al., 1991a,b) and is not an effective means for dissociating calving difficulty, birth weight, and growth. Use of complementarity by mating terminal sire breeds to older, maternal breed cows and by mating specialized sire lines (or breeds) selected for direct calving ease to heifers and young cows does reduce the conflict between faster growth and larger calves with more difficult births. Even so, the relationship between birth weight and postnatal growth among breeds limits the choice of terminal sire and maternal breeds that can be used. Within-breed selection for increased growth and reduced calving difficulty is clearly possible and is an approach that should be very useful for interbreeding and rotational mating systems.

The most important result from this study is the clear demonstration of substantial genetic variation in heifer calving difficulty score and birth weight that is partially independent of yearling weight and that can be selected by using multiple-trait EBV technology. An ad hoc EBV selection procedure was used in this study, but any selection procedure (e.g., index, linear programming, culling levels, etc.) based on EBV should produce similar changes if it results in EBV selection differentials that are proportional to the changes in this experiment. However, weighting of EBV for use by the cattle industry should be based on economic principles. This study demonstrates that appropriately weighted EBV should produce the desired and predicted results even though traits might be complicated or antagonistic. This result is expected to apply generally to other antagonistically correlated traits important to beef cattle production, such as carcass quality and carcass yield.

Conclusions

Selection for reduced heifer calving difficulty score breeding value with either no change or increased yearling weight breeding values was successful. Breeding values were calculated from a multiple-trait animal model including a subjective difficulty score, birth weight, weaning weight, and postweaning gain. These traits are currently collected by several breed associations. When calculated by using multiple-trait models, breeding values for these traits can be used to make desired changes, even when traits are complicated or are moderately but undesirably correlated.

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